

The crocodilian *Theriosuchus* Owen, 1879 in the Wealden of England

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Synopsis

A skull fragment from the Wealden of Brook (Isle of Wight) is described and referred to the genus *Theriosuchus* Owen, 1879, previously known from the Purbeck of England. A little-known previous report of *Theriosuchus* teeth from the Wealden is discussed. Isolated procoelous vertebrae from the English Wealden named *Heterosuchus valdensis* by Seeley and often referred to the enigmatic crocodilian *Hylaeochampsia* may actually belong to *Theriosuchus*.

Introduction

This paper reports the previously overlooked occurrence of the crocodilian *Theriosuchus* in the Wealden of England. The genus *Theriosuchus* was erected by Owen in 1879, with *T. pusillus* as type species, for remains of a small crocodilian found by W. H. Beckles in the Purbeck Beds of Dorset. *Theriosuchus* may be a genus of great importance in crocodilian evolution. Its systematic position was interpreted variously before Joffe (1967) showed that it closely resembled the Atoposauridae from the Upper Jurassic of Europe, and suggested it should be included in that family. She also noted that *Theriosuchus* was very progressive in some respects (palatal structure, procoelous vertebrae) and might have been close to the ancestry of the Eusuchia, or have evolved in parallel with them. Although basically I agree with Joffe's conclusions, I think *Theriosuchus* may be sufficiently divergent from the typical Atoposauridae to warrant its inclusion in a separate family, as already suggested by Kälin in 1955 (see Buffetaut, 1982, for a more complete discussion).

The fossil reptile collection of the British Museum (Natural History) contains a fairly large number of remains of *Theriosuchus pusillus* from the 'Feather Bed' of the Middle Purbeck (see Joffe, 1967, for more details). However, apart from a very brief report, apparently overlooked by all later authors, which will be discussed below, there was until now no record of *Theriosuchus* from other localities.

In September 1980 Dr Peter Wellnhofer (Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich) was examining the Hooley collection of pterosaurs from the Wealden of the Isle of Wight in the British Museum (Natural History). While doing so he came across the fragmentary posterior part of the skull of a small crocodilian (reg. no. R.176), and later he kindly mentioned this to me. Although very incomplete, the specimen turned out to be identifiable as *Theriosuchus*.

Previous report of *Theriosuchus* from the Wealden

At first it was thought that this skull fragment was the first find of *Theriosuchus* in the Wealden, but a careful search through the literature revealed that the genus had already been reported from this formation. In 1912 there appeared in *Nature* a very short anonymous news item on fossils recently presented to the British Museum (Natural History), which is quoted here in full:

The Geological Department of the British Museum (Natural History) has also recently received a valuable gift of Wealden fossils from the Revs P. Teilhard and F. Pelletier, S.J., who made the collection during a four years' residence near Hastings. A large proportion of the specimens are small teeth from bone-beds

which had previously been very little examined, and among them is the unique mammalian tooth described under the name of *Dipriodon valdensis* by Dr Smith Woodward in 1911. There are numerous teeth of the dwarf crocodile *Theriosuchus*, which has hitherto been known only from the Purbeck beds. The series of plant-remains is also important and will shortly be described by Prof. A. C. Seward in a communication to the Geological Society.

In the discussion following the 1911 paper by Woodward on the above-mentioned mammal tooth, Charles Dawson had mentioned that Teilhard de Chardin and Pelletier (who were then studying theology at Hastings) had been helping him for two years in his researches on the Wealden bone beds of the Hastings area.

The report in *Nature* went unnoticed, and I have been unable to find any later mention of *Theriosuchus* in the Wealden. The isolated teeth in question are kept in the British Museum (Natural History) under the collective numbers R.4424–31 inclusive. They come mainly from the Wadhurst Clay and the Ashdown Clay of Fairlight West, although some were collected near Brede (both localities in the vicinity of Hastings). Similar teeth (R.3697) were presented even earlier, in 1909, by Charles Dawson.

Some of these teeth are not especially characteristic, being of the usual crocodilian type, conical and pointed; they cannot really be identified with any accuracy. Others are more distinctive, being laterally compressed, with a low, rather blunt crown, which is somewhat leaf-shaped in profile; these are very reminiscent of the posterior teeth of *Theriosuchus pusillus*. However, supplementary and more convincing evidence for the occurrence of *Theriosuchus* in the Wealden of England is provided by the present skull fragment.

The skull fragment R.176

The skull fragment found by Dr Wellnhofer in the Hooley collection (Fig. 1) comes from the Wealden of Brook (also spelt Brooke) on the southern coast of the Isle of Wight. A detailed description of the Wealden section at Brook Bay is given by Osborne White, who mentions

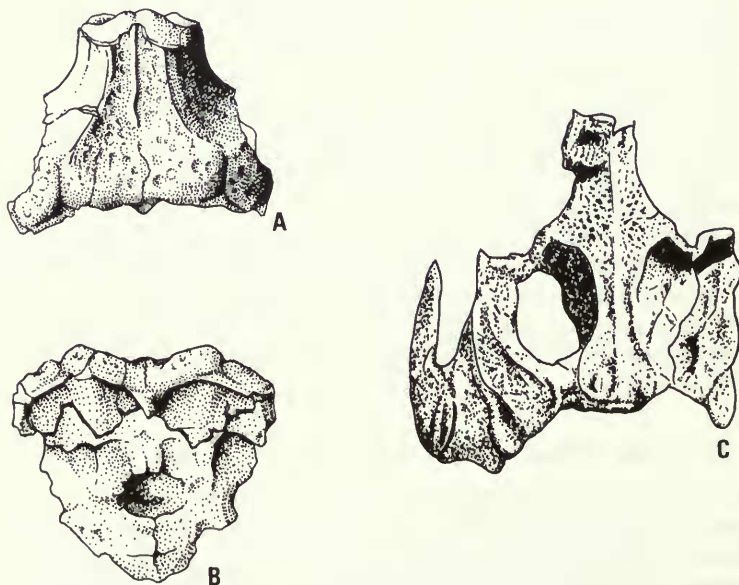


Fig. 1 A, B: Skull fragment of *Theriosuchus* sp. indet. from the Wealden of Brook, Isle of Wight, BM(NH)R.176, in dorsal (A) and posterior (B) views. C: posterior part of the skull of *Theriosuchus pusillus* from the Purbeck of Dorset, BM(NH) 48216, in dorsal view, for comparison (after Owen, 1879). All $\times 1$. Drawings A and B by Dominique Visset.

(1921: 8) that 'the Wealden Beds of Brook Bay have yielded the remains of various large reptiles, including *Iguanodon bernissartensis* Boul., *Hoplosaurus hulkei* (Seeley), and *Heterosuchus valdensis* Seeley'. Incidentally, *Heterosuchus valdensis* is by no means a large reptile, but a small crocodilian, of which more will be said below.

The skull fragment comprises the greater part of the parietal, small medial portions of the squamosals, and parts of the bones of the occipital region (supraoccipital, exoccipitals, basioccipital); however, the occipital surface is poorly preserved, being much crushed and cracked. The lateral surfaces of the braincase are also very poorly preserved.

What is left of the parietal is roughly trapezoidal in outline, the bone becoming increasingly wider towards the rear. It is definitely narrower (7 mm) between the upper temporal fenestrae than farther posteriorly (maximum width 22 mm). Anteriorly, the parietal is incomplete, but apparently not much is missing. The dorsal surface of the bone is distinctly concave transversely, especially in its posterior part, as can readily be seen in posterior view. The anterolateral edges of the parietal are raised into blunt ridges, which extend forwards and become narrower between the upper temporal fenestrae. The dorsal surface of the bone is ornamented with small irregular pits. An interesting feature is the presence of a very well marked, fairly sharp, median ridge, which extends along the entire length of the bone. Posteriorly, the parietal overhangs the occipital surface. On this surface, there is a prominent triangular median tuberosity or spine, which seems to be formed partly by the parietal and partly by the supraoccipital. Only the dorsal part of the latter bone is preserved; it shows a pair of depressions, one on either side of the above-mentioned spine. More ventrally, the bones are so crushed that little is discernible; the site of the foramen magnum is still visible, but the occipital condyle has disappeared. When the dorsal surface of the parietal is placed in a horizontal plane, the occipital surface is seen to be sloping forwards at an angle of about 60°, a condition more primitive than in modern crocodilians (in which the occipital plane is nearly vertical), but not so archaic as in many mesosuchians. The occipital surface seems to have been high relative to its width. As mentioned above, little is left of the squamosals. A remarkable feature is the presence of a fairly deep and very distinct groove between the parietal and the squamosals. The latter seem to have had relatively well developed posterior expansions; in dorsal view, the posterior edge of the skull roof is distinctly concave.

Although fragmentary, this specimen exhibits several features present in *Theriosuchus pusillus*, suggesting its reference to the same genus. The shape of the parietal is very similar, although its posterior part is wider in the Wealden specimen than in those from the Purbeck. The lateral ridges on the parietal also occur in *Theriosuchus pusillus*, and the sharp median ridge is a constant feature of all specimens from the Purbeck. The grooves between the parietal and the squamosals are present both in the fragment from Brook and in *Theriosuchus pusillus*. The ornamentation of the skull table of the Wealden specimen is very reminiscent of that of the Purbeck form. Comparison of the occipital surfaces is hardly possible, since that region, although not much flattened, is poorly preserved in the Wealden fossil, while all the Purbeck specimens are strongly compressed dorsoventrally.

The Wealden specimen is somewhat larger than the type of *Theriosuchus pusillus*, but it still indicates a small animal. Joffe (1967) suggested that most of the specimens of *Theriosuchus pusillus* were juveniles, but this seems doubtful. Her evidence was based partly on a single femur from the Purbeck referred to *Theriosuchus pusillus*, larger than other femora of the species. However, the femur can hardly be called a very diagnostic bone in crocodilians, and the specimen in question may not belong to *Theriosuchus*. The allegedly juvenile characters of the skull of *Theriosuchus pusillus* listed by Joffe are observable also in the Atoposauridae from continental Europe, which, according to Wellnhofer (1971), are not juveniles. It should also be mentioned that the crocodilian obviously related to *Theriosuchus* briefly described (but not yet named) by Langston (1974) from the 'Comanchean' (Lower Cretaceous) of Texas is hardly larger than the type of *Theriosuchus pusillus*. The Wealden specimen described here also suggests that *Theriosuchus* and its allies may never have grown to a large size.

The resemblances to *Theriosuchus pusillus* listed above indicate that the skull fragment from the Wealden of Brook should be referred to the genus *Theriosuchus*. However, the specimen is

too incomplete to warrant a specific identification and I think it better to designate it as *Theriosuchus* sp. indet.

Stratigraphical range of *Theriosuchus*

The skull fragment from the Wealden of Brook provides the first really convincing evidence of the occurrence of *Theriosuchus* in the Lower Cretaceous of England, and thus extends its stratigraphical range, previously limited to the Purbeckian. This of course is only a small extension, since the Middle Purbeck beds which have yielded *Theriosuchus pusillus* are only slightly below the Jurassic–Cretaceous boundary as defined in Dorset by Casey (1963). According to Casey, the limit lies within the Purbeck beds, at the base of the 'Cinder Bed'. As shown by Joffe (1967), *Theriosuchus pusillus* comes from the 'Feather Bed', about 10 ft (3 m) below the 'Cinder Bed'. The time-span separating the Wealden *Theriosuchus* from the Late Jurassic *Theriosuchus pusillus* is certainly not very great.

The occurrence of *Theriosuchus* in the Wealden beds is not really unexpected, since the crocodilian faunas of the Purbeck and of the Wealden have several other elements in common (notably *Goniopholis crassidens* and *G. simus*, as well as the genus *Pholidosaurus*). *Theriosuchus* can now be added to the list of crocodilians known from the Wealden of England, which already includes the genera *Goniopholis*, *Pholidosaurus*, *Vectisuchus* (described by Buffetaut & Hutt, 1980) and *Bernissartia* (reported by Buffetaut & Ford, 1979).

Theriosuchus and *Heterosuchus*

Seeley (1887) described as *Heterosuchus valdensis* a series of procoelous vertebrae in a small nodule from the Hastings Sands of Hastings, which had been collected by Gideon Mantell and is now in the collections of the British Museum (Natural History) under reg. no. 36555. He also referred to this species 'a few isolated vertebrae of similar character' from the Wealden of Tilgate and of Brook, also collected by Mantell and later purchased by the British Museum. More isolated procoelous vertebrae from the Wealden were later referred to *Heterosuchus valdensis* by Lydekker (1888).

Lydekker (1887) suggested that the vertebrae named *Heterosuchus* by Seeley might actually belong to *Hylaeochampsa vectiana*, a peculiar crocodilian described by Owen (1874) from the Wealden of the Isle of Wight. *Hylaeochampsa vectiana* is known by a single incomplete skull, in which the internal nares are in a typical eusuchian position (i.e. totally enclosed by the pterygoids) and which shows a peculiar construction of the palate, with large openings in the ectopterygoids. The phylogenetic and systematic positions of *Hylaeochampsa* are still doubtful (Buffetaut 1975), as it is uncertain whether it is closely related to modern eusuchians or is the result of convergent evolution. Many authors have followed Lydekker's suggestion that *Heterosuchus* is probably a junior synonym of *Hylaeochampsa* (Kälin 1955, von Huene 1956, Romer 1956, 1966, Steel 1973). However, the skull of *Hylaeochampsa* was not associated with vertebrae, and the only reason to assume that the vertebrae of *Heterosuchus* belong with the skull of *Hylaeochampsa* is that in the Eusuchia skulls with internal nares in a position similar to that of *Hylaeochampsa* are associated with procoelous vertebrae like those of *Heterosuchus*. It should nevertheless be remembered that the evolution of a modern type of palate need not have been synchronous with that of procoelous vertebrae. This is beautifully shown by *Theriosuchus pusillus*, in which, as pointed out by Joffe (1967), there are already procoelous vertebrae, while the palate is still of advanced mesosuchian type. Similarly, the *Theriosuchus*-like crocodilian from Texas mentioned by Langston (1974) has an advanced mesosuchian palate and procoelous vertebrae. Since *Theriosuchus* is now known to occur in the Wealden of England, one may reasonably suppose that at least some of the procoelous vertebrae found in the same beds belong to that genus rather than to *Hylaeochampsa*. The latter may have had procoelous vertebrae, but this remains to be demonstrated by the discovery of associated skull and vertebral material.

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References

- Anonymous** 1912. [Wealden fossils presented to British Museum by Revs P. Teilhard and F. Pelletier, S.J.] *Nature, Lond.*, **90**: 111.
- Buffetaut, E.** 1975. Sur l'anatomie et la position systématique de *Bernissartia fagesii* Dollo, L., 1883, Crocodilien du Wealdien de Bernissart, Belgique. *Bull. Inst. r. Sci. nat. Belg.*, Brussels, (sci. terre) **51** (2): 1–20, 4 pls.
- 1982. Radiation évolutive, paléoécologie et biogéographie des Crocodiliens méso-suchiens. *Mém. Soc. géol. Fr.*, Paris, (n.s.) **60** (142): 1–88.
- & **Ford, R. L. E.** 1979. The crocodilian *Bernissartia* in the Wealden of the Isle of Wight. *Palaeontology*, London, **22** (4): 905–912.
- & **Hutt, S.** 1980. *Vectisuchus leptognathus*, n.g. n.sp., a slender-snouted goniopholid crocodilian from the Wealden of the Isle of Wight. *Neues Jb. Geol. Paläont. Mh.*, Stuttgart, **1980** (7): 385–390.
- Casey, R.** 1963. The dawn of the Cretaceous period in Britain. *Bull. S.-east. Un. scient. Socs.*, Tunbridge Wells, **117**: 1–15.
- Huene, F. von** 1956. *Paläontologie und Phylogenie der niederen Tetrapoden*. 716 pp. Jena.
- Joffe, J.** 1967. The 'dwarf' crocodiles of the Purbeck Formation, Dorset: a reappraisal. *Palaeontology*, London, **10** (4): 629–639.
- Kälin, J.** 1955. Crocodilia. In Piveteau, J. (ed.), *Traité de Paléontologie*, **5**: 695–784. Paris.
- Langston, W.** 1974. Nonmammalian Comanchean tetrapods. *Geosci. Man*, Baton Rouge, **8**: 77–102.
- Lydekker, R.** 1887. Note on *Hylaeochampsia*. *Geol. Mag.*, London, **4**: 512–513.
- 1888. *Catalogue of the fossil Reptilia and Amphibia in the British Museum (Nat. Hist.)*, **I**. xxviii + 309 pp. London.
- Osborne White, H. J.** 1921. *A short account of the geology of the Isle of Wight*. 219 pp. London (Mem. geol. Surv. U.K.).
- Owen, R.** 1874–79. Monograph on the fossil Reptilia of the Wealden and Purbeck Formations. Supplement no. VI, Crocodilia (*Hylaeochampsia*). 7 pp. and pl. II of Suppl. V. *Palaeontogr. Soc. (Monogr.)*, London (1874). Supplement no. IX. Crocodilia (*Goniopholis*, *Brachydectes*, *Nannosuchus*, *Theriosuchus* and *Nuthetes*). 19 pp., 4 pls. *loc. cit.* (1879).
- Romer, A. S.** 1956. *Osteology of the reptiles*. 772 pp. Chicago & London.
- 1966. *Vertebrate Paleontology* (3rd edn). 468 pp. Chicago & London.
- Seeley, H. G.** 1887. On *Heterosuchus valdensis* Seeley, a procoelian crocodile from the Hastings Sand of Hastings. *Q. Jl geol. Soc. Lond.*, **43**: 212–215.
- Steel, R.** 1973. Crocodylia. In Kuhn, O. (ed.), *Handbuch der Paläoherpetologie*, **16**. 116 pp. Stuttgart & Portland.
- Wellnhofer, P.** 1971. Die Atoposauridae (Crocodylia, Mesosuchia) der Oberjura-Plattenkalke Bayerns. *Palaeontographica*, Stuttgart, (A) **138** (5–6): 133–165.
- Woodward, A. S.** 1911. On some mammalian teeth from the Wealden of Hastings. *Q. Jl geol. Soc. Lond.* **67**: 278–281.